PhytoKeys

PhytoKeys 237: 91–102 (2024)
DOI: 10.3897/phytokeys.237.114105

Research Article

# Re-evaluating monotypic *Eleutherostylis* from New Guinea and the Moluccas and its inclusion in *Grewia* (Malvaceae, Grewioideae)

Laurence J. Dorr[1], Kenneth J. Wurdack[1]

1 *National Museum of Natural History, Department of Botany, MRC-166, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012, USA*
*Corresponding author: Laurence J. Dorr (dorrl@si.edu)*

## Abstract

Morphological and molecular phylogenetic evidence indicate that *Eleutherostylis* Burret (Malvaceae, Grewioideae), a monotypic genus described from New Guinea, is best considered a synonym of *Grewia* L., a species-rich genus widespread across the Paleotropics and found in Africa, Arabia, Asia, Australia and the western Pacific. A new combination, based on *E. renistipulata* Burret, *G. renistipulata* (Burret) Dorr, **comb. nov.**, is proposed. Original material of the basionym could not be located and a neotype is designated. A lectotype is designated for *G. morotaiensis* Kosterm., a synonym of *G. renistipulata*.

**Key words:** *Eleutherostylis*, *Grewia*, lectotype, Malvaceae, neotype, phylogeny

OPEN ACCESS

**Academic editor:** S. K. Ganesan
**Received:** 12 October 2023
**Accepted:** 18 December 2023
**Published:** 19 January 2024

**Citation:** Dorr LJ, Wurdack KJ (2024) Re-evaluating monotypic *Eleutherostylis* from New Guinea and the Moluccas and its inclusion in *Grewia* (Malvaceae, Grewioideae). PhytoKeys 237: 91–102. https://doi.org/10.3897/phytokeys.237.114105

**Copyright:** © L. J. Dorr & K. J. Wurdack. This is an open access article distributed under the terms of the CC0 Public Domain Dedication.

## Introduction

Generic circumscriptions in Malvaceae s.l. remain surprisingly unsettled and many genera of clearly uncertain circumscription have not had their monophyly tested in well-sampled phylogenies. Sufficient taxon sampling in such phylogenies, even with limited genetic loci, can often identify problems and suggest alternative taxonomies (e.g. *Eriolaena* DC., see Dorr and Wurdack (2021)). *Grewia* L. (Malvaceae, Grewioideae), one of the largest genera in the family, with 280–300 species distributed across Africa, Arabia, Asia, Australia and the western Pacific has a history of generic circumscription problems with multiple segregates. One of those segregates, the monotypic genus *Eleutherostylis* Burret, endemic to New Guinea and the Moluccas, is the focus of this study. When Burret (1926) created *Eleutherostylis*, he stated how it differed from *Grewia* while tacitly admitting the two genera were closely allied. He observed that his new genus differed by having several styles that are free to the base and a gynoecium with more locules. *Eleutherostylis* has 4(5) locules while *Grewia* sensu Burret has 1–2(3) locules. These two genera along with *Vincentia* Bojer (non Gaud.) and *Microcos* L. were the only genera Burret (1926) included in his circumscription of Grewieae Endl. (Grewioideae).

Hutchinson (1967) retained *Eleutherostylis* in an expanded circumscription of Grewieae in which he included seven genera. His concept of the genus *Grewia* included *Vincentia* Bojer and *Microcos* as synonyms rather than distinct genera. In Hutchinson's (1967) key to the tribe, *Eleutherostylis* was distinguished from

*Grewia* by a single character, viz. flowers dioecious versus flowers bisexual. Earlier, Burret (1926) had rather pointedly dismissed floral sexuality as a useful systematic character ("Systematischer Wert ist [die Geschlechtsverh] nicht beizumessen"). Hutchinson also noted that he did not follow Burret (1926) who retained *Vincentia* Bojer and *Microcos* as genera separate from *Grewia* because the "stigmatic characters used for distinguishing [these two genera] are scarcely of generic importance". The former is considered now a synonym of *Grewia* (Capuron and Mabberley 1999) while there is strong evidence the latter is distinct (see Brunken and Muellner (2012)).

Few other authors have discussed the relationships of *Eleutherostylis*. Kostermans (1972) considered the genus to be close to both *Grewia* and *Trichospermum* Blume and he placed *G. morotaiensis* Kosterm., described from the Moluccas, in synonymy under *E. renistipulata*. Bayer and Kubitzki (2003) maintained *Eleutherostylis* as a distinct genus, separating it from *Grewia* by the lack of a style in female flowers (versus styles cylindrical or dilated apically) and its heteromorphic (versus usually monomorphic) stipules. The latter is scarcely a generic character and positionally varies within a plant (heteromorphic pairs of reniform plus filiform stipules on lateral plagiotropic branches, but only reniform stipules on orthotropic branches). Brunken and Muellner (2012) included *Eleutherostylis* in their circumscription of the Grewieae and within that tribe in their "Grewia subclade". They based their argument on a morphological phylogenetic analysis, but did not elaborate on either characters or relationships within the subclade they recognised, which also included *Colona* Cav., *Desplatsia* Bocq., *Mollia* Mart., *Tetralix* Griseb. and *Trichospermum*, based on molecular data and *Duboscia* Bocq. and *Vasivaea* Baill., based solely on morphological data. Their phylogenetic analysis did not support the inclusion of *Eleutherostylis* within *Grewia*, although there was not strong support for any of the relationships that they found. Jennings (2021) treated *Eleutherostylis* in a floristic account of the trees of New Guinea, but the key couplet in that work used to separate *Eleutherostylis* from *Grewia* is based only on leaf and stipule characters.

Pollen data presented by Perveen et al. (2004) do not permit one to distinguish *Eleutherostylis* from *Grewia*. The pollen grains of both are described as coarsely reticulate and 3-colporate. The pollen shape ratio (P/E) of the former (1.66) falls within the range (1.27–2.05) of the limited number of species sampled of the latter. Pollen grains of both genera, prolate with long colpi, are described as "Corchorus-type", which can be applied to most Grewioideae, except for *Apeiba* Aubl., which Brunken and Muellner (2012) placed in Apeibeae Benth., a tribe distinct from Grewioideae. Hoorn et al. (2019), relying on the information and images provided by Perveen et al. (2004), noted that, within Malvaceae, the occurrence of prolate–subprolate bireticulate pollen with long colpi and distinct margos is restricted to Grewioideae.

*Eleutherostylis* was recently sampled with genomic-scale data for the Plant and Fungal Trees of Life Project (PAFTOL) and it was resolved as the strongly-supported sister-group to the single *Grewia* sampled (*G. flavescens* Juss.) (see Tree of Life Explorer, https://treeoflife.kew.org/tree-of-life; Baker et al. (2022)). The PAFTOL generic-exemplar approach to taxon sampling, however, did not test the monophyly of *Grewia*, which requires a more synoptic representation for that genus. The goals of our study, as part of broader phylogenetic work within Grewioideae, were to test the relationships of *Eleutherostylis* more adequately with respect to *Grewia*.

## Material and methods

The taxon sampling here of 107 tips was a subset of data from an ongoing broader phylogenetic study and included *Eleutherostylis renistipulata* (*Schodde & Craven 4438*, US [01210662], the neotype designated below), along with a wide geographic sampling of *Grewia* (61 species) and 23/25 genera of Grewioideae (missing *Erinocarpus* Nimmo ex J. Graham and *Goethalsia* Pittier, which have been sampled elsewhere) recognised by Bayer and Kubitzki (2003). Outgroups included three Byttnerioideae (Malvaceae). Appendix 1 provides details of data sources, including vouchers and GenBank accession numbers. The nuclear ribosomal Internal Transcribed Spacer (ITS) region was selected for its ability to resolve the relevant taxa and recoverability from herbarium-specimen sourced DNAs. While single/few locus phylogenetic studies may appear dated in this genomics era, they remain appropriate for the scale of questions addressed here. Molecular methods for the 97 newly-generated sequences and phylogenetic analyses largely followed Dorr and Wurdack (2021) from DNeasy Plant Mini Kit (Qiagen Inc., Valencia, California, USA) extractions through to fluorescent Sanger sequencing of ITS amplification products on an ABI 3730xl DNA Analyzer (Thermo Fisher Scientific, Waltham, Massachusetts). The multiple sequence alignment (MSA) used MAFFT v.7.272 (Katoh and Standley 2013) under the G-INS-i refinement method, followed by minor manual refinements, based on a similarity criterion. Sensitivity analyses with different MAFFT optimality criteria, alignment without the divergent Byttnerioideae outgroups and exclusion sets to reduce missing data (i.e. removal of 119 MSA columns with > 50% missing data that reduced overall missing data from 16.2 to 3.85%) had little impact on the phylogenetic resolution, except in a few poorly-supported nodes. While there is sequence length variation within *Grewia*, there are few ambiguously aligned regions within our sampling for the genus. The MSA with the tested exclusion set is archived in the Dryad data repository (https://doi.org/10.5061/dryad.cnp5hqcbx). Final Maximum Likelihood (ML) analyses using all data were with IQ-TREE v.1.6.12 (Trifinopoulos et al. 2016) under GTR+F+I+G4 (selected by ModelFinder; Kalyaanamoorthy et al. (2017)) and RAxML-NG (Stamatakis 2014) as implemented on CIPRES XSEDE under GTR+I+Γ and clade support estimated by 1000 rapid bootstrap replicates. Bayesian Inference (BI) under GTR+I+Γ was performed using MrBayes v.3.2.7a (Ronquist et al. 2012) with two concurrent runs, each with four Markov chains (three cold and one heated), a 0.2 temperature coefficient and sampling every 1000 generations over 50 million generations and a conservative 25% burn-in. Topology and support value differences between the ML programmes were slight (IQ-TREE values are presented in Fig. 1); however, more pronounced were ML versus BI differences with shifts in some deeper nodes (albeit mostly poorly supported).

## Results

*Eleutherostylis* is resolved as well-nested with multiple strongly-supported nodes (Posterior probability = 1.0, ML bootstrap > 85%) within a paraphyletic *Grewia* (Fig. 1). Its sequence divergence is relatively high amongst *Grewia* species, although it does not present additional alignment problems. Relationships within *Grewia* suggest a complex biogeography, although the small taxon and gene

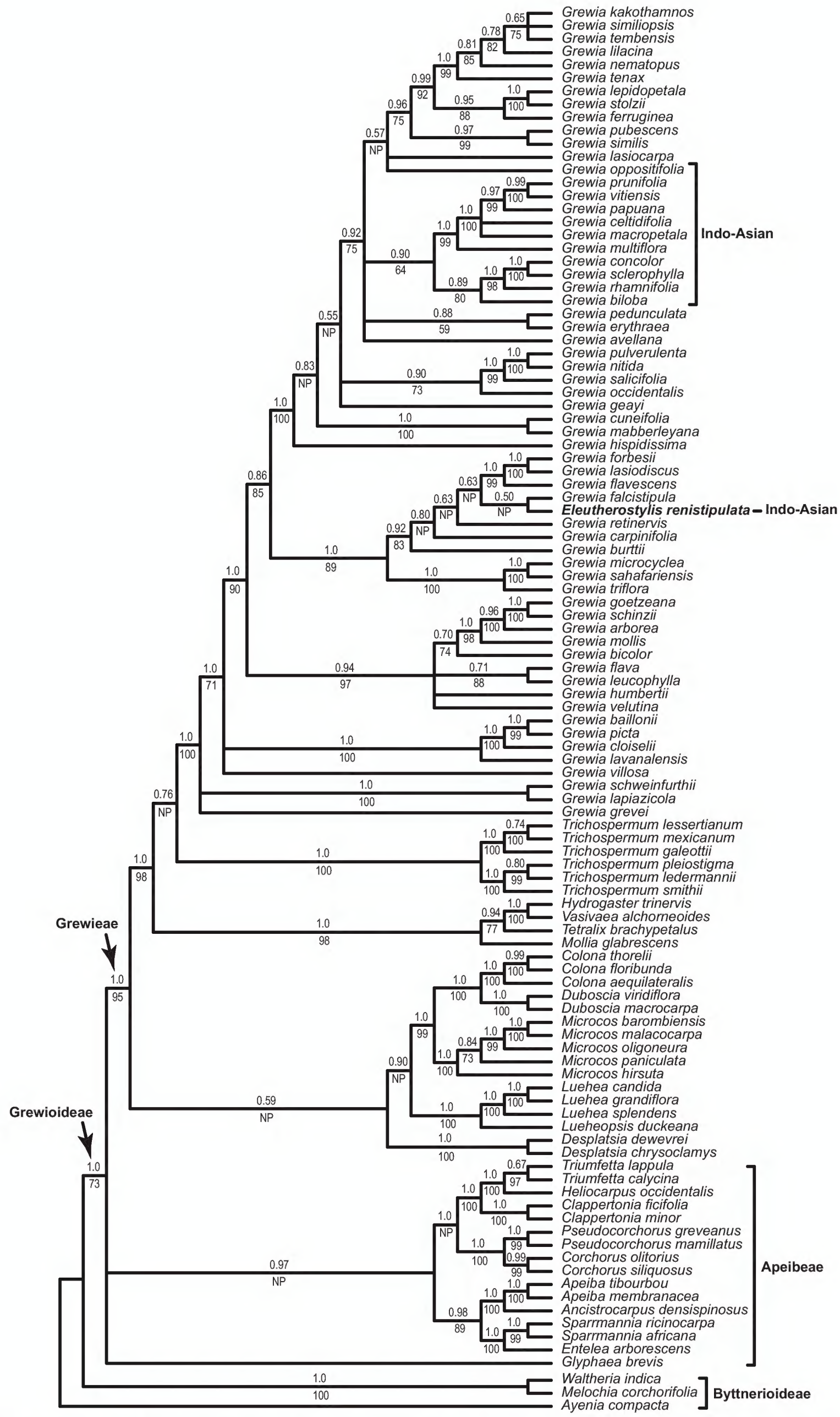


**Figure 1.** Phylogenetic relationships of *Eleutherostylis* and its Grewioideae relatives. Bayesian 50% majority-rule consensus tree, based on ITS sequences with posterior probability and IQ-TREE ML bootstrap values indicated, above and below branches, respectively. NP = an edge not present with ML.

sampling presented here limit our conclusions. The *Grewia* subclade containing *Eleutherostylis* contains only African species, while all the other Indo-Asian species (11 sampled) are far removed and mostly in a separate well-supported subclade. Relationships amongst the genera of Grewioideae and resolution as two major clades (circumscribed as tribes Apeibeae and Grewieae) largely mirror other studies (Bayer et al. 1999; Brunken and Muellner 2012; PAFTOL), except in the weakly-supported placement here of *Desplatsia* further removed from *Grewia*. *Microcos* is clearly distinct from *Grewia* and groups with *Colona* and *Duboscia*, which are Asian and African genera, respectively. *Desplatsia* and *Duboscia*, both African, are distinct from each other despite prior uncertainty (see Bayer and Kubitzki (2003)). The Neotropical and Palaeotropical taxa of *Trichospermum* group as separate sister subclades.

## Discussion

*Grewia* is a morphologically diverse and biogeographically interesting genus, with species radiations in the Paleotropics, especially in sub-arid and woodland regions of Africa with 60% of the nearly 300 species. This diversification of arid-adapted shrubby species, often with animal dispersed fleshy drupaceous fruit, is especially notable in Madagascar (ca. 65 species, mostly endemic) and Sub-Saharan Africa (124 species) (Gautier et al. 2012). The Indo-Asian (including China) diversity of *Grewia* contains ca. 73 species, with a subset of only 28 species in the Flora Malesiana Region (Peninsula Malaysia, Indonesia, New Guinea, Philippines and Borneo). The relatively isolated nature of *Eleutherostylis* is suggested by sequence divergence and its placement amongst African taxa away from the Indo-Asian clade. However, our limited taxon sampling (ca. 20% of *Grewia* species) and limited phylogenetic resolution prevent us from reliably identifying finer patterns in biogeography, except to note that the Malagasy endemics do not form a monophyletic group. While *Eleutherostylis* fits well within the broad morphological diversity of *Grewia*, it is ecologically unusual in the genus inasmuch as it is a large dioecious tree with dry fruit in lowland tropical forests. Most Malvaceae are hermaphroditic and dioecy is rare. Within Grewioideae, dioecy characterises *Hydrogaster* Kuhlm., *Tetralix*, *Vasivaea* and some *Grewia* (including *Eleutherostylis*). In addition, *Erinocarpus*, *Grewia*, *Heliocarpus* L. and *Triumfetta* L. have some species with alternative breeding systems (e.g. polygamous, gynodioecious) and sometimes unisexual (staminate, pistillate) flowers. While the stipules of *Eleutherostylis* are conspicuous because of their relatively largely size and positional dimorphism, similar large stipules occur in other species of *Grewia* (e.g. *G. falcistipula* K. Schum., an African species).

### Taxonomic summary

***Grewia renistipulata* (Burret) Dorr, comb. nov.**
urn:lsid:ipni.org:names:77334716-1
Fig. 2

*Eleutherostylis renistipulata* Burret, Notizbl. Bot. Gart. Berlin-Dahlem 9(88): 630. 1926. Type: New Guinea. Gulf District: West bank of Vailala River, ca. 3 mi south of junction with Lohiki River, ca. 18 m elev., 3 Feb 1966 (fl, fr),

*R. Schodde & L.A. Craven 4438* (neotype, here designated: US [01210662]!; isoneotypes: A-2 sheets!, BH!, BO, BRI, CANB [162189.1], CANB [162190.3], CANB [162191.2], G, K [K000062278 as image!], L [L.2349560 as image!], LAE, PNH).

*Grewia morotaiensis* Kosterm., Reinwardtia 7(5): 444, fig. 5. 1969 (p. 444 as "*raorotaiensis*"; fig. 5 as "*morotaiensis*"). Type: Indonesia. Moluccas, Morotai Isl., Distr. Tobelo near Totodoku [sic], 30 m elev., 2 May 1949 (fr), *A.J.G.H. Kostermans & W. Tangkilisan 44* (= *bb 33752*) (lectotype, here designated: [BO-1331873 as image!]; isolectotypes: A, BM, BO [BO-1331874 as image!], K, L [L 0062741 as image!], LAE, P, PNH, SING [0054550]).

**Additional specimens examined.** INDONESIA. Moluccas, Morotai, Subdistr. Tobelo, north near Totodokoe, 30 m elev., 9 May 1949 (fl), *A.J.G.H. Kostermans & W. Tangkilisan 101* (= *bb 33795*) (A, BO [BO-1331875 as image!], K, L [L.2349554 as image!], L [L.2349555 as image!], SING). NEW GUINEA. [Papua New Guinea]. Gulf District, Delta Divn., Baroi Riv., near Port Romilly, 26 Feb 1951, *M.F.C. Jackson 4119* (BISH, BRI, L [L.2349551 as image!], LAE). Madang District: ca. 5 km SE of Faita Village, along the Ramu River, ca. 150 m elev., 29 Jul 1955 (fl), *R.D. Hoogland 5044* (BRI, CANB [76047.1], CANB [76047.2], L [L.2349552 as image!], L [L.2349561 as image!], LAE, MEL [MEL 2370751A]!). Madang District, Gogol Base, 18 Aug 1969 (♂), *M. Kumul W. 2672* (A!, L [L.2349562 as image!]). INDONESIA [Netherlands New Guinea]. Hollandia, 29 Oct 1954 (fr), *A. Brower Bw. 1611* (L [L.2349558 as image!], LAE). Sekoli Plain, Div. Hollandia, ca. 100 m elev., 25 Feb 1960, *G. Th. Iwanggin BW 9206* (BISH (×2), CANB [518317.1], L [L.2349557 as image!], WAG [WAG.1834811 as image!], WAG [WAG.1834812 as image!]). Sekoli- Plain, Div. Hollandia, ca. 100 m elev., 26 Feb 1960, *G. Th. Iwanggin BW 9222* (BISH, CANB [51833.1], L [L.2349564 as image!], LAE). Hollandia, Berap (Nimboeran), 9 Aug 1939, *Neth. Ind. For. Service bb.28959* (L [L.2349556 as image!]). W. Irian, Dozai, E. of Sukarnapura (= Hollandia), 50 m elev., 24 Aug 1966 (♂), *A.J.G.H. Kostermans & W. Soegeng 554* (CANB [339882.1], L [L.2349559 as image!]). Sekoli, O. Afd. Hollandia, 75 m elev., 26 Feb 1960, *A. Noesi BW 8147* (L [L.2349563 as image!], LAE). Tami, Hollandia, 19 Jan 1955, *F. Schram BW 1639* (CANB [51612.1], L [L.2349553 as image!], LAE).

**Nomenclatural notes.** Burret (1926) based *Eleutherostylis renistipulata* on two collections (syntypes) made by C.L. Ledermann in Sepik, Papua New Guinea: *Ledermann 10535* with male flowers and *Ledermann 10754* with female flowers and fruit. Neither of these syntypes, which were in Berlin (B), survived World War II (Juraj Paule, pers. comm.; see also Hiepko (1987)). Steenis-Kruseman (1950, 1958) noted that, in addition to Ledermann collections deposited in B, duplicate material sometimes can be found in E, K, L and SING, but no duplicates of the syntypes have been located in these Herbaria. Hence, the designation here of a neotype for the name (Fig. 2).

Kostermans (1969) used two different epithets in the original description of *Grewia morotaiensis*: "raorotaiensis" in the text and "morotaiensis" in the figure caption. These epithets have equal priority. Subsequently, Kostermans (1972) effectively made a choice between these competing epithets when he placed *G. morotaiensis* in synonymy under *Eleutherostylis renistipulata* (see Turland et al. (2018; Art. 11.5)).

Eleutherostylis renistipulata Burret
det @ Arnold Arbor.
FLORA OF NEW GUINEA
Distributed by the
HERBARIUM AUSTRALIENSE, C.S.I.R.O., CANBERRA, A.C.T.
with the request to be notified of new identifications.
Coll. R. Schodde (and L. A. Craven)
No. 4438 Date 3 Feb. 1966
fam. Tiliaceae Grewia
West bank of Vailala river, ca 3 miles south of junction with Lohiki river, Gulf District.
Primary alluvial forest; alt. ca 60 feet.
Tree ca 37 m high, trunk unbuttressed; bark smooth flaky dark brown, blaze biscuit cream; wood pale cream; leaves dull glossy mid green above, paler below; corollas and fruit green cream.
Wood sample collected.
Specimens in CANB,LAE,L,A,K,BRI,US,BO,PNH, G,BH.
Image No.
01210662
UNITED STATES
2894118
NATIONAL HERBARIUM

**Figure 2.** Neotype of *Eleutherostylis renistipulata* Burret (US [01210662]).

## Acknowledgements

We thank Gabriel Johnson (US) for generating much of the ITS data and MO and US for relevant specimens.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Funding

The molecular phylogenetic work was conducted with support from the Laboratories of Analytical Biology (LAB) of the National Museum of Natural History, Smithsonian Institution.

### Author contributions

Conceptualization: LJD, KJW. Formal analysis: KJW. Investigation: KJW, LJD. Methodology: KJW. Writing – original draft: LJD. Writing – review and editing: KJW, LJD.

### Author ORCIDs

Laurence J. Dorr https://orcid.org/0000-0001-7157-363X
Kenneth J. Wurdack https://orcid.org/0000-0003-0010-6932

### Data availability

All of the data that support the findings of this study are available in the main text or were deposited in archives (Dryad or GenBank).

## References

Baker WJ, Bailey P, Barber V, Barker A, Bellot S, Bishop D, Botigué LR, Brewer G, Carruthers T, Clarkson JJ, Cook J, Cowan RS, Dodsworth S, Epitawalage N, Françoso E, Gallego B, Johnson MG, Kim JT, Leempoel K, Maurin O, McGinnie C, Pokorny L, Roy S, Stone M, Toledo E, Wickett NJ, Zuntini AR, Eiserhardt WL, Kersey PJ, Leitch IJ, Forest F (2022) A comprehensive phylogenomic platform for exploring the Angiosperm Tree of Life. Systematic Biology 71(2): 301–319. https://doi.org/10.1093/sysbio/syab035

Bayer C, Fay MF, De Bruijn AY, Savolainen V, Morton CM, Kubitzki K, Alverson WS, Chase MW (1999) Support for an expanded family concept of Malvaceae within a recircumscribed order Malvales: A combined analysis of plastid *atp*B [sic] and *rbc*L [sic] DNA sequences. Botanical Journal of the Linnean Society 129(4): 267–303. https://doi.org/10.1111/j.1095-8339.1999.tb00505.x

Bayer C, Kubitzki K (2003) Malvaceae. In: Kubitzki K, Bayer C (Eds) The Families and Genera of Vascular Plants. V. Flowering Plants. Dicotyledons. Malvales, Capparales and non-betalain Caryophyllales. Springer-Verlag, Berlin, 225–311. https://doi.org/10.1007/978-3-662-07255-4_28

Brunken U, Muellner NA (2012) A new tribal classification of Grewioideae (Malvaceae) based on molecular phylogenetic evidence. Systematic Botany 37(3): 699–711. https://doi.org/10.1600/036364412X648670

Burret M (1926) Beiträge zur Kenntnis der Tiliaceen. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9(88): 592–880. https://doi.org/10.2307/3994327

Capuron R, Mabberley DJ (1999) Révision des Malvaceae-Grewioideae ("Tiliacées", p.p.) de Madagascar et des Comores. III. Les *Grewia* du sous-genre *Vincentia* (Benth.) Capuron. Adansonia, sér. 3, 21(1): 7–23. https://biostor.org/reference/245092

Dorr LJ, Wurdack KJ (2021) Indo-Asian *Eriolaena* expanded to include two Malagasy genera, and other generic realignments based on molecular phylogenetics of Dombeyoideae (Malvaceae). Taxon 70(1): 99–126. https://doi.org/10.1002/tax.12370

Gautier L, Chatelain C, Callmander MW, Phillipson PB (2012) Richness, similarity and specificity of Madagascar flora compared with Sub-Saharan Africa. Plant Ecology and Evolution 145(1): 55–64. https://doi.org/10.5091/plecevo.2012.591

Hiepko P (1987) The collections of the Botanical Museum Berlin-Dahlem (B) and their history. Englera 7: 219–252.

Hoorn C, van der Ham R, de la Parra F, Salamanca S, ter Steege H, Banks H, Star W, van Heuven BJ, Langelaan R, Carvalho FA, Rodríguez-Forero G, Lagomarsino LP (2019) Going north and south: The biogeographic history of two Malvaceae in the wake of Neogene Andean uplift and connectivity between the Americas. Review of Palaeobotany and Palynology 264: 90–109. https://doi.org/10.1016/j.revpalbo.2019.01.010

Hutchinson J (1967) The Genera of Flowering Plants (Angiospermae), Dicotyledones (Vol. 2). Clarendon Press, Oxford.

Jennings LVS (2021) Malvaceae subfam. Grewioideae Dippel (Malvaceae). In: Utteridge TMA, Jennings LVS (Eds) Trees of New Guinea. Kew Publishing, Royal Botanic Gardens, Kew, 427–431.

Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14(6): 587–589. https://doi.org/10.1038/nmeth.4285

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kostermans AJGH (1969) New and critical Malesian plants VIII. Reinwardtia 7(5): 433–449.

Kostermans AJGH (1972) A synopsis of the Old World species of *Trichospermum* Blume (Tiliaceae). Transactions of the Botanical Society of Edinburgh 41(3): 401–430. https://doi.org/10.1080/03746607208685242

Perveen A, Grafström E, El-Ghazaly G (2004) World pollen and spore flora 23. Malvaceae Adams. [sic] P.p. Subfamilies: Grewioideae, Tilioideae, Brownlowioideae. Grana 43(3): 129–155. https://doi.org/10.1080/00173130410000730

Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Trifinopoulos J, Nguyen L-T, von Haeseler A, Minh BQ (2016) W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44(W1): W232–W235. https://doi.org/10.1093/nar/gkw256

Turland NJ, Wiersema JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF [Eds] (2018) International Code of Nomenclature for algae, fungi, and plants

(Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten. https://doi.org/10.12705/Code.2018

van Steenis-Kruseman MJ (1950) Malaysian plant collectors and collections being a cyclopaedia of botanical exploration in Malaysia and a guide to the concerned literature up to the year 1950. Flora Malesiana, ser. 1, 1: 1–639.

van Steenis-Kruseman MJ (1958) Malaysian plant collectors and collections. Suppl. I. Flora Malesiana, ser. 1 5: 1–108. [CCXXV-CCXLII]

## Appendix 1

Vouchers

Sources for data used in the phylogenetic analysis of Grewioideae. Ordered as: Taxon, Voucher (new data only; bc = barcode) and GenBank number (new data begin with OR).

*Ancistrocarpus densispinosus* Oliv., Cameroon, *X. van der Burgt et al. 936* (MO-6147053) OR934538. *Apeiba membranacea* Spruce ex Benth., Bolivia, *E. Stijfhoorn 705* (US-3266700; bc 0053551), OR934539. *Apeiba tibourbou* Aubl., Bolivia, *S. Paredes 427* (US-3684178; bc 01183679), OR934540. *Ayenia compacta* Rose, MF963978. *Clappertonia ficifolia* (Willd.) Decne., Ghana, *D. Harder et al. 3447* (MO-5030390), OR934541. *Clappertonia minor* (Baill.) Bech., Ghana, *H. Schmidt et al. 2081* (MO-5019391), OR934542. *Colona aequilateralis* (C.T.White & W.D.Francis) Merr. & L.M.Perry, New Guinea, *L. Craven & R. Schodde 1014* (US-3320995; bc 01317130), OR934543. *Colona floribunda* (Kurz) Craib, KR531939 (ITS2 only). *Colona thorelii* (Gagnep.) Burret, KR531940 (ITS2 only). *Corchorus olitorius* L., KY968914. *Corchorus siliquosus* L., FJ527604. *Desplatsia chrysochlamys* (Mildbr. & Burret) Mildbr. & Burret, Central African Republic, *D. Harris & J. Fay 680* (US-3404805; bc 01210682), OR934544. *Desplatsia dewevrei* (De Wild. & T.Durand) Burret, Uganda, *ATBP 572* (MO-4935375), OR934545. *Duboscia macrocarpa* Bocq., Gabon, *J. Reitsma & B. Reitsma 2260* (NY), OR934546. *Duboscia viridiflora* (K.Schum.) Mildbr., Ghana, *C. Jongkind et al. 1807* (MO-4667359), OR934547. *Eleutherostylis renistipulata* Burret, New Guinea, *R. Schodde & L. Craven 4438* (US-2894118; bc 01210662), OR934548. *Entelea arborescens* R.Br., FR875089. *Glyphaea brevis* (Spreng.) Monach., Ghana, *H. Schmidt et al. 1618* (MO-504354), OR934549. *Grewia arborea* (Forssk.) Lam., Tanzania, *P. Kuchar 24804* (MO-5688296), OR934550. *Grewia avellana* Hiern, Namibia, *S. Rugheimer et al. 2980* (US-3702461; bc 01183956), OR934551. *Grewia baillonii* R. Vig., Madagascar, *R. Noyes et al. 1011* (MO-5054318), OR934552. *Grewia bicolor* Juss., Namibia, *L. Nanyeni 311* (US-3702456; bc 01183964), OR934553. *Grewia biloba* G. Don, China, *D. Boufford et al. 37887* (MO-6139773), OR934554. *Grewia burttii* Exell, Tanzania, *P. Kuchar 23193* (MO-5583151), OR934555. *Grewia carpinifolia* Juss., Ghana, *C. Jongkind 1707* (MO-4666899), OR934556. *Grewia celtidifolia* Juss., China, *L. Heng 8587* (MO-5320749), OR934557. *Grewia cloiselii* R.Vig., Madagascar, *T. Croat 31963* (MO-2599538), OR934558. *Grewia concolor* Merr., China, *N. Chun & C. Tso 44606* (US-1675394; bc 01173074), OR934559. *Grewia cuneifolia* Juss., Madagascar, *R. Gereau et al. 5733* (US-3335856; bc 00833950), OR934560. *Grewia erythraea* Schweinf., Ethiopia, *D.*

*Sebsebe & A. Berhanu 1996* (MO-3887915), OR934561. *Grewia falcistipula* K. Schum., Namibia, *S. Bartsch et al. 1800* (US-3599415; bc 00814074), OR934562. *Grewia ferruginea* Hochst. ex A.Rich., Tanzania, *S. Bidgood et al. 3492* (MO-4925265), OR934563. *Grewia flava* DC., Namibia, *S. Rugheimer et al. 2504* (US-3702462; bc 01183961), OR934564. *Grewia flavescens* Juss., Namibia, *S. Rugheimer et al. 2669* (US-3702455; bc 01183967), OR934565. *Grewia forbesii* Harv. ex Mast., Tanzania, *R. Gereau et al. 6624* (MO-5334011), OR934566. *Grewia geayi* R.Vig., Madagascar, *F. Chauvet 397* (MO-6332845), OR934567. *Grewia goetzeana* K.Schum., Tanzania, *A. Ntemi Sallu 665* (MO-5753794), OR934568. *Grewia grevei* Baill., Madagascar, *P. Phillipson 1680* (MO-3514731), OR934569. *Grewia hispidissima* Wahlert et al., Madagascar, *J. Razafitsalama & Torze 1091* (US-3547850; bc 01205465), OR934570. *Grewia humbertii* Capuron, Madagascar, *P. Phillipson 2536* (MO-3662965), OR934571. *Grewia kakothamnos* K.Schum., Ethiopia, *C. Puff 870423-315* (MO-4010325), OR934572. *Grewia lapiazicola* Capuron, Madagascar, *M. Bardot-Vaucoulon & G. Véné 1782* (MO-6152266), OR934573. *Grewia lasiocarpa* E.Mey. ex Harv., South Africa, *P. Phillipson 4381* (MO-5650943), OR934574. *Grewia lasiodiscus* K.Schum., Mali, *C. Duvall 91* (MO-5333223), OR934575. *Grewia lavanalensis* Baill., Madagascar, *P. Phillipson 3092* (US-3398970; bc 01205481), OR934576. *Grewia lepidopetala* Garcke, Tanzania, *Y. Abeid et al. 1860* (MO-4797160), OR934577. *Grewia leucophylla* Capuron, Madagascar, *P. Phillipson & S. Rabesihanaka 3143* (US-3398976; bc 01205489), OR934578. *Grewia lilacina* K.Schum., Tanzania, *V. Simon & Y.S. Abeid 69* (MO-4902872), OR934579. *Grewia mabberleyana* Phillipson et al., Madagascar, *G. Schatz 3356* (MO-6719378), OR934580. *Grewia macropetala* Burret, China, *Qin Hai-ning et al. 2362* (MO-5746218), OR934581. *Grewia microcyclea* (Burret) Capuron & Mabb., Madagascar, *P. Phillipson 2908* (US-3404759; bc 01207518), OR934582. *Grewia mollis* Juss., Tanzania, *F. Mawi et al. 182* (MO-5731705), OR934583. *Grewia multiflora* Juss., Burma, *R. Belcher* [*US Typhus Comm.*] *671* (US-2213169; bc 00685866), OR934584. *Grewia nematopus* K. Schum., Kenya, *Y. Harvey et al. 60* (MO-5779207), OR934585. *Grewia nitida* Juss., Madagascar, *G. McPherson et al. 14761* (MO-3771574), OR934586. *Grewia occidentalis* L., South Africa, *G. Germishuizen 952* (US-3022273; bc 01207559), OR934587. *Grewia oppositifolia* Buch.-Ham. ex DC., India, *W. Koeltz 4446* (US-1608157; bc 01173134), OR934588. *Grewia papuana* Burret, Australia, *G. Batianoff 900146* (MO-4341230, OR934589. *Grewia pedunculata* K.Schum., Mozambique, *W. Luke et al. 9907* (MO-5761031), OR934590. *Grewia picta* Baill., Comoros, *J.-N. Labat 3198* (MO-6113815), OR934591. *Grewia prunifolia* A.Gray, Fiji, *A. Smith 7910* (US-2190725; bc 00813934), OR934592. *Grewia pubescens* P.Beauv., Guinea, *C. Jongkind 8345* (MO-6185625), OR934593. *Grewia pulverulenta* R.Vig., Madagascar, *G. McPherson & N. Dumetz 14317* (MO-3771579), OR934594. *Grewia retinervis* Burret, Namibia, *L. Hoffman 568* (US-3702466; bc 01183958), OR934595. *Grewia rhamnifolia* B.Heyne ex Roth, Sri Lanka, *A. Robyns 7209* (US-2660528; bc 00813779), OR934596. *Grewia sahafariensis* Capuron & Mabb., Madagascar, *R. Capuron 23036-SF* (MO-6354013), OR934597. *Grewia salicifolia* Schinz, Seychelles (Aldabra), *S. Renvoize 1346* (US-2779483; bc 01207633), OR934598. *Grewia schinzii* K.Schum., Botswana, *P. Smith 4360* (MO-5988288), OR934599. *Grewia schweinfurthii* Burret, Ethiopia, *D. Sebsebe & B. Tamirat 2349* (MO-3855548), OR934600. *Grewia sclerophylla* Roxb. ex G.Don, Nepal, *R. Troth 704* (US-2826357; bc 01173161), OR934601. *Grewia similiopsis*

C.Whitehouse, Tanzania, *P. Kuchar 24245* (MO-5700280), OR934602. *Grewia similis* K.Schum., Tanzania, *L. Ellemann 645* (MO-4859391), OR934603. *Grewia stolzii* Ulbr., Tanzania, *J. Lovett & C. Kayombo 4389* (US-3362978; bc 01207665), OR934604. *Grewia tembensis* Fresen., Saudi Arabia, *T. Miyazaki 990915R5* (MO-6334153), OR934605. *Grewia tenax* (Forssk.) Fiori, Namibia, *H. Kolberg et al. 1215* (US-3702464; bc 01183955), OR934606. *Grewia triflora* (Bojer) Walp., Madagascar, *F. Ratovoson et al. 916* (MO-6034468; bc MO-1059913), OR934607. *Grewia velutina* (Forssk.) Lam., Saudi Arabia, *T. Miyazaki 990905R1* (MO-6334157), OR934608. *Grewia villosa* Willd., Saudi Arabia, *J. Lavranos & I. Collenette 20449* (MO-2952050), OR934609. *Grewia vitiensis* Turrill, Fiji, *O. Degener 15242* (US-1944019; bc 00980012), OR934610. *Heliocarpus occidentalis* Rose, Mexico, *R. McVaugh 20863* (US-2151641; bc 00520160), OR934611. *Hydrogaster trinervis* Kuhlm., Brazil, *J. Paixao et al. 554* (NY-884904), OR934612. *Luehea candida* (DC.) Mart., Mexico, *J. Amith 1843* (US-3635420; bc 00976739), OR934613. *Luehea grandiflora* Mart., Brazil, *B. Amorim et al. 523* (US-3645266; bc 01183510), OR934614. *Luehea splendens* Rusby, Bolivia, *R. López & M. Capra 825* (US-3670168; bc 01183716), OR934615. *Lueheopsis duckeana* Burret, Brazil, *G. Árboez et al. 4305* (US-3419295; bc 00727607), OR934616. *Melochia corchorifolia* L., MH768329. *Microcos barombiensis* (K.Schum.) Cheek, Cameroon, *X. van der Burgt & J. Amambo 379* (MO-5779211), OR934617. *Microcos hirsuta* (Korth.) Burret, Indonesia, *C. Peters 1025* (US-3290456; bc 01208471), OR934618. *Microcos malacocarpa* (Mast.) Burret, Ghana, *H. Schmidt et al. 2022* (MO-5006532), OR934619. *Microcos oligoneura* (Sprague) Burret, Gabon, *J. Boussengui-Nongo 281* (MO-6311890), OR934620. *Microcos paniculata* L., KP092996. *Mollia glabrescens* Benth., Guyana, *K. Redden et al. 6241* (US-3572625; bc 01074205), OR934621. *Pseudocorchorus greveanus* (Baill.) Capuron, Madagascar, *J. & M. Peltier 5196* (MO-6356087), OR934622. *Pseudocorchorus mamillatus* Capuron, Madagascar, *R. Bolliger 337* (MO-6612809), OR934623. *Sparrmannia africana* L.f., South Africa, *R. Brand 228* (MO-5652084), OR934624. *Sparrmannia ricinocarpa* (Eckl. & Zeyh.) Kuntze, FR875088. *Tetralix brachypetalus* Griseb., Cuba, *R. Berazaín et al. [JBNC] 71840* (NY), OR934625. *Trichospermum galeottii* (Turcz.) Kosterm., Mexico, *P. Acevedo-Rdgz. et al. 16062* (US-3697233, bc: 01343493), OR934626. *Trichospermum ledermannii* Burret, Palau (Caroline Islands), *F. Fosberg 50600* (US-3408397; bc 01165395), OR934627. *Trichospermum lessertianum* (Hochr.) Dorr, Mexico, *G. Martínez Calderón 1651* (US-3571535; bc 00976860), OR934628. *Trichospermum mexicanum* (DC.) Baill., Mexico, *J. Amith 1817 (*US-3635429; bc: 00976741), OR934629. *Trichospermum pleiostigma* (F. Muell.) Kosterm., Papua New Guinea, *W. Takeuchi 4559* (US-3306729 [sic] US-3716430 bc: 04214468), OR934630. *Trichospermum smithii* Kosterm., Fiji, *J. Gressitt 2499* (US-2210382; bc: 00977330), OR934631. *Triumfetta calycina* Turcz., Peru, *W. Galiano et al. 4835* (US-3534756; bc 00755457), OR934632. *Triumfetta lappula* L., Panama, *P. Peterson & C. Annable 7242* (US-3114850; bc 00501649), OR934633. *Vasivaea alchorneoides* Baill., Guyana, *M. Jansen-Jacobs et al. 34* (US-3070508; bc 00513683), OR934634. *Waltheria indica* L., MH768330.